Effects of Oak-hickory Woodland Restoration Treatments on Native Groundcover Vegetation and the Invasive Grass, *Microstegium vimineum* ⧉

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ABSTRACT

An important goal of restoring fire to upland oak-dominated communities that have experienced fire exclusion is restoring groundcover plant species diversity and composition indicative of fire-maintained open habitats. Treatment-driven declines in rare forest specialists and increases in widespread ruderals and competitive non-native species, however, could negate the benefits of ecological restoration in these ecosystems. We tested the effects of treatment-related disturbances on native groundcover vegetation, density and proliferation of patches of an invasive grass, Japanese stiltgrass (*Microstegium vimineum*), and the net effects of treatment and the invasive grass on native groundcover vegetation. Results from multiple years of monitoring at two replicate sites in north Mississippi showed that thinning and burning significantly increased both groundcover species richness and the abundance of species indicative of fire-maintained open habitats. We found subtle increases in forest species in response to treatments, whereas most native ruderals did not increase significantly in response to the treatments over the long term. The density and competitive effect of the invasive Japanese stiltgrass increased dramatically at both sites in response to the restoration treatments. However, new patches of Japanese stiltgrass established in response to the treatments only at the site with the more recent history of agricultural disturbance. Results suggest that fire restoration treatments were effective in the absence of past agricultural disturbance and in areas lacking Japanese stiltgrass. At sites with a history of agriculture and large populations of Japanese stiltgrass, effective restoration may require eradication of Japanese stiltgrass and reintroduction or augmentation of competitive, native specialists of fire-maintained open habitats.

Keywords: canopy gap, competition, fire, habitat fidelity, species richness

🔥 Restoration Recap 🔥

- There is disagreement and uncertainty among ecologists and land managers regarding the appropriate role of fire in mesic, oak-dominated forests.
- Elimination of offsite tree species from the canopy and selective thinning of oaks, combined with biennial prescribed burning in the spring, effectively increased groundcover plant diversity and the abundance of species indicative of fire-maintained open woodlands in a mesic oak-dominated forest in north Mississippi.

- Although most native and non-native ruderals did not respond positively to restoration, Japanese stiltgrass (a highly invasive, non-native grass) did.
- Practitioners could use selective thinning and prescribed burning to restore groundcover plant diversity and desired species composition in oak-hickory forests, especially at sites that contain native, open woodland indicators and that lack Japanese stiltgrass or a recent history of soil disturbance.

Throughout much of eastern North America, modern fire exclusion efforts have converted plant communities that previously were open habitats dominated by fire-tolerant tree species to more-or-less closed-canopy upland forests containing a mix of fire-tolerant and mesophytic species (Nowacki and Abrams 2008). During the periods of early European settlement and before in the eastern

and southern United States, fire frequency in many oak-dominated portions of the upland landscape was greater than observed following modern fire suppression in the 20th century (Van Lear and Waldrop 1989, Delcourt and Delcourt 1998, Guyette and Spetich 2003, Hart et al. 2008, Spetich et al. 2011). Although direct accounts of ground-cover plant species composition prior to modern fire exclusion are scarce, many such communities are thought to have contained highly diverse groundcover plant communities in the past. Modern fire exclusion (in addition to other land use changes) is believed to have resulted in dramatic losses of plant diversity in these ecosystems (Smith 1994, Taft 1997, Bowles and McBride 1998, Hutchinson et al. 2005, Surrette and Brewer 2008, Brewer and Menzel 2009).

In addition to fire-maintained open habitats, significant portions of the early-settlement landscape in the eastern United States were dominated by mesophytic species with low tolerance of fires. In contrast to most fire-dependent ecosystems, most mesic forests were restricted to fire refugia such as rich floodplains and terraces, steep mesic ravines, and loess bluffs with deep fertile soils (Braun 1950, Delcourt and Delcourt 1977, Grimm 1984, Schwartz 1994, Brewer 2001, Surrette et al. 2008). Except for areas near human settlements (Delcourt 1987, Patterson and Sassaman 1988, Guyette and Cutter 1997, Platt and Brantley 1997), conditions were likely not conducive to fires of sufficient severity or frequency to limit the establishment of fire-sensitive tree species (Beilmann and Brenner 1951, Grimm 1984). Because of the fertile soils associated with some of these mesic and alluvial communities, many of these sites have been converted to agriculture, resulting in losses of groundcover plant diversity (Bellemare et al. 2002, Flinn and Velland 2005). Hence, like fire-maintained open habitats, forests dominated by fire-sensitive, mesophytic species have been dramatically altered, but would most likely benefit from protection from frequent or intense fires (Mola et al. 2014). Both community types warrant serious consideration for protection and/or ecological restoration to maintain biodiversity.

The benefits or consequences of prescribed burning in upland mesic deciduous forests exclusive of terraces, bluffs, and ravines are poorly understood. Frequent fires are known to have occurred in at least some of these communities during early Euro-American settlement (e.g., Surrette et al. 2008). Nevertheless, restoring such fire regimes as a means of restoring a prior ecosystem state (i.e., environmental legacy, sensu Clewell and Aronson 2013), regardless of whether one considers it to be a "natural" state, may not be feasible (Clewell and Aronson 2013). Although prescribed burning has the potential to provide an important service to society by reducing the risk of dangerous and destructive wildfires (Fernandes and Botelho 2003), reduced flammability following prolonged fire exclusion in deciduous forests of the eastern United States may have decreased the incidence of intense wildfires in this region

(Nowacki and Abrams 2008). Consequently, prescribed burning, by itself, may be of limited utility in reducing hazardous fuels in forests of this region (Brewer and Rogers 2006). Therefore, to a large degree, the decision to restore historic fire regimes to upland mesic forests of the eastern United States that have experienced modern fire exclusion should be based on effects on biological diversity, ecological complexity, and capacity for self-organization (ecological recovery, sensu Clewell and Aronson 2013). To that end, restoring an approximation of historic fire regimes may be effective at achieving ecological recovery, but controlled experiments are necessary for verification.

Restoring historical fire regimes to upland mesic forests that have experienced modern fire exclusion could be justified if it reverses declines in rare, fire-dependent species and does not have the unintended consequence of increasing widespread ruderals or invasives or decreasing regionally rare, fire-sensitive species (Brawn 2006, Brewer and Menzel 2009). We hypothesize that such beneficial effects of restoring historical fire regimes are likely if the following four conditions hold: 1) historical fire regimes (regardless of their cause: lightning, Native Americans, early European settlers) previously eliminated most fire-intolerant species from uplands and favored fire-tolerant species; 2) modern fire exclusion has not completely eliminated fire-dependent species from uplands and has not significantly benefited fire-sensitive species that are rare or threatened; 3) historical fire regimes largely consisted of low-intensity surface fires that favored long-lived fire-tolerant perennials and not opportunistic ruderals or invasives that typically require more intense disturbances for successful establishment (Grime 1979, Roberts 2007, Brewer and Bailey 2014); and 4) the primary cause of degradation is fire exclusion and not more severe perturbations (i.e., agricultural soil disturbance). We hereafter refer to the positive responses of groundcover vegetation to the restoration of historical fire regimes under these conditions as the fire tolerance hypothesis. On the other hand, some upland areas that historically experienced frequent fires have been subjected to fire suppression for so long that they have lost many fire-tolerant species, transitioned to an alternative stable state, and reached a point of no return (Nowacki and Abrams 2008). Such losses of fire-tolerant species are more likely to occur in areas with relatively fertile soils, where canopy closure is likely to have been rapid. Upland areas with fertile soils are also more likely to have had a recent history of agriculture, which could favor invasive species and ruderals, while having a negative effect on fire-tolerant long-lived perennials (Surrette and Brewer 2008). If attempts at restoring fire in these areas largely benefit invasive species and widespread ruderals and have a negative effect on rare or declining forest species that benefitted from fire suppression, then prescribed burning in these areas would be ill advised (Keeley 2006, Matlack 2013). We refer to this alternative hypothesis as the disturbance sensitivity hypothesis.

One invasive species in particular that could be problematic for fire restoration is Japanese stiltgrass (*Microstegium vimineum*), an annual C4 grass originating from East Asia that occurs in deciduous forests throughout much of the eastern US (Fairbrothers and Gray 1972). This species is arguably one of the most problematic in terms of management of deciduous forests in the eastern United States (Flory 2010). Previous experiments have revealed positive responses to fire and canopy openings (Glasgow and Matlack 2007, Emery et al. 2013) and competitive suppression of groundcover vegetation and tree seedlings (Flory and Clay 2010a, Aronson and Handel 2011, Brewer 2011). The fact that this competitive species is able to tolerate the shade of the forest interior but also respond positively to canopy disturbance and fire suggests that any positive effects of canopy disturbances and fire on native species could be negated by its positive responses to restoration treatments. We are not aware of any studies, however, that have examined the net effects of fire restoration and Japanese stiltgrass abundance on native groundcover vegetation.

In the current study, we test the predictions of the fire tolerance and disturbance sensitivity hypotheses by examining the effects of canopy reduction and prescribed burning on groundcover vegetation changes in two long-unburned upland hardwood forests subjected to fire restoration in the mesic loess plains of northern Mississippi (USA). We specifically addressed the following four questions: 1) how do groundcover plant species richness and abundance respond to combined canopy reduction and biennial prescribed fire?; 2) how do plants indicative of fire-maintained open habitats (hereafter, open-habitat species [i.e., those in open habitats]), closed-canopy forests (hereafter, forest species [i.e., those in forests]), and severe anthropogenic disturbance, (hereafter, ruderals [i.e., those in disturbed habitats]) differ in their responses to combined canopy reduction and prescribed burning?; 3) how do density and the number of patches of the invasive grass, Japanese stiltgrass, respond to canopy reduction and prescribed burning; and 4) what are the net responses of native groundcover vegetation to treatments within patches of Japanese stiltgrass?

Methods

Study Area

An oak-hickory woodland restoration experiment was initiated in 2003 at Strawberry Plains Audubon Center (hereafter, Strawberry Plains), a 1,000-ha sanctuary located in the loess plains of north-central Mississippi. The loess plains are characterized by gently rolling hills with moderately fertile, mesic silt and sandy loams in the uplands and floodplains. The experiment was a paired design (adjacent 1 ha treated and control areas) replicated at each of two upland mesic sites several kilometers apart (the Wildflower Loop site [34°49′60″ N, 89°28′32″ W]; the Sharecropper

Loop site [34°49′52″ N, 89°27′17″ W]). Both sites contained a mixture of silt loam alfisols and sandy loam ultisols, with silt loam predominating at Wildflower Loop, and sandy loam predominating at Sharecropper Loop (Morris 1981, Maynard and Brewer 2013). At the beginning of the experiment, both sites contained closed-canopy (> 90% overstory canopy coverage), mature oak-hickory-sweetgum-elm forests (100 + years old Wildflower Loop, 50 + years with scattered 100 + year-old trees at Sharecropper Loop), long protected from fire. Dominant overstory and midstory tree species included southern red oak (*Quercus falcata*), post oak (*Q. stellata*), black oak (*Q. velutina*), white oak (*Q. alba*), blackjack oak (*Q. marilandica*), mockernut hickory (*Carya tomentosa*), sweetgum (*Liquidambar styraciflua*), black gum (*Nyssa sylvatica*), and winged elm (*Ulmus alata*) (Brewer 2014). Aerial photos from the early 1960s revealed that the forest at Sharecropper Loop was more open than at Wildflower Loop, with the former showing some signs of soil erosion caused by prior cotton agriculture dating back to the 1800s.

Experimental Design

Tree species locally absent or rare (as tree-sized individuals) in uplands historically (i.e., "offsite" species, e.g., sweetgum, winged elm, blackgum, black cherry [*Prunus serotine]*, red maple [*Acer rubrum*]) were thinned in the treated plots beginning in 2004 at Wildflower Loop and late 2007 at Sharecropper Loop (see Brewer 2001 and Surrette et al. 2008 for descriptions of early 19th century tree species distributions in north-central Mississippi). All offsite tree species with stems greater than 10 cm basal diameter were cut or girdled and treated with Pathway herbicide (picloram and 2-4-D). No stems of flowering dogwood (*Cornus florida*) were cut or girdled, due to the small size of this species and uncertainty regarding its historical presence within upland woodlands in northern Mississippi. To reduce overstory canopy tree densities of "onsite" species to levels comparable to those seen in the early 19th century (Brewer 2001), approximately one-half of overstory stems (greater than 25 cm dbh) of southern red oak, white oak, and mockernut hickory were killed using girdling and herbicide. Such thinning treatments reduced canopy closure by ~15%. Treated plots were burned approximately every other year, primarily in the spring (March or April). Specifically, at Wildflower Loop (established in 2003), treated plots were burned in March or April 2005, 2010, 2012, and 2014. In addition, grassy edges of the treated plot at Wildflower Loop were burned in the summer or early fall of 2004, 2006, and 2008. The treated plot at Sharecropper Loop was burned in March or April in 2010 and 2012 and a grassy edge of it was burned in the summer of 2008. Because of the inability to get summer or early fall fires to carry through the plots beyond the edge (due to inadequate fuels and high humidity), summer/fall burning was discontinued after 2008. The control plot at

Wildflower Loop was burned in March 2004. Initially, this plot was intended to be a burn-only treatment, but was converted to a control plot after the original control plot was damaged by road construction in 2009. This control plot was accidentally burned again in April 2014 as a result of the prescribed fire in the adjacent treated plot escaping containment (data for the spring 2014 census for this plot were therefore not included in analyses). The control plot at Sharecropper Loop has not been burned for as long as available records indicate. The treated plot at that site was not burned as scheduled in spring 2014.

Groundcover Vegetation Surveys

Existing groundcover vegetation plots established in 2003 (Wildflower Loop) and 2007 (Sharecropper Loop) were revisited and censused in 2009, 2010, 2012, and 2013. Groundcover plants were defined as all herbaceous species, all stems of shrubs less than 1 m tall, and all tree seedlings less than 1 m tall. Basal sprouts (< 1 m tall) from topkilled saplings (woody stems > 1 m tall) were not considered groundcover vegetation in this study and were analyzed separately in a previous study (Brewer 2014). The censuses for each of these years consisted of a fall census, which captured most identifiable species, and a subsequent early-April census of the following year (to capture spring ephemerals and winter annuals). Initial censuses involved approximate counts of all groundcover plant species within 10×30 m subplots nested within adjacent treated and control plots (~0.6 to 7.4 ha) at each of the two sites. Initially, there were three subplots within the treated plot and two subplots in the control plot at Wildflower Loop, and one subplot each in the treated and control plots at Sharecropper Loop. Beginning in 2009, more precise counts of stems or clumps were conducted in several (4 to 13) 1.5 m × 1.5 sub-subplots nested within the 10 m × 30 m subplots. An additional subplot was added to the treated and control plots in 2011. By 2011, all plots contained at least one 10 × 30 m subplot in the upper portion of the slope and one 10 × 30 m subplot on the lower portion of the slope. The treated plot at Wildflower Loop contained two upper-slope subplots. The number of sub-subplots per subplot established depended on the level of species diversity within the subplot encountered in 2009 (or 2011), as assessed from species-area curves. More diverse subplots (e.g., the treated subplots at Wildflower Loop) contained more sub-subplots to obtain a more representative sample of the groundcover vegetation within the subplot. To ensure a representative sample of the number of species within each plot, statistical analyses of species richness were based on estimated expected numbers of species derived from species-area curves within each plot and used the experimental error (plot-level) term with 1 df (2 sites and 2 treatment levels).

Groundcover species composition within sub-subplots (or subplots in 2003 or 2007) was quantified by density (counts of stems or clumps of all species) and fidelity of the sub-subplot assemblage to open habitats, forests, and disturbed habitats. Habitat fidelity calculations were derived from weighted averages of abundances of all species, wherein the weights were species-specific habitat indication scores. Details of the calculation are described in Brewer and Menzel (2009) and Brewer et al. (2012) and in Appendix 1. In short, a species' habitat indication score was derived from the proportional similarity in species composition between those specific habitats in the region in which the species occurred (as determined from regional flora manuals) and species composition of the general habitat category of interest (e.g., open or forests or disturbed), again as determined by regional flora manuals (see Appendix 1, Supplementary Tables).

Statistical analyses of density (log-transformed after adding 1 to avoid taking the log of zero) and habitat indication in 2013 were done using nested analysis of variance using a Restricted Expected Maximum Likelihood approach. Sub-subplot error was nested within subplot error, which was nested within treatment and site. Tests of site and treatment effects were done using the subplot error term. Because of unequal sample sizes, analyses were conducted using Type II sums of squares, assuming no site × treatment interaction ($p > 0.2$). A separate analysis was done for the initial censuses using subplot values averaged across the plot and using the site × treatment interaction as the error term.

Surveys of Japanese Stiltgrass Patches

Japanese stiltgrass, though common in forests at Strawberry Plains and present within the sites of the current study, was absent from groundcover vegetation plots in this study. Therefore, beginning in 2007, thorough searches for patches of Japanese stiltgrass (clumps of more 20 plants within a ~4-m² area) were conducted throughout each treated and control plot at each site to monitor changes in density within patches and the proliferation or disappearance of patches in response to the treatments. A 4-m² circular sampling patch was established, containing each clump of plants. Counts of Japanese stiltgrass were made at the time of patch establishment and then repeated yearly in the fall and spring until 2014. In very dense patches (i.e., > 500 stems), total density was estimated by systematically locating eight points within the patch and measuring the distance between each point and the closest Japanese stiltgrass stem (Cottam and Curtis 1956). Changes in abundance of Japanese stiltgrass were analyzed statistically by first taking the difference of natural-log transformed densities per m² for the initial and final census for each patch and then analyzing the effects of treatment, site, and the treatment by site interaction using patch variation nested within site and treatment as the error term. Treatment and site effects on the rate of patch proliferation of Japanese stiltgrass were examined statistically using randomization tests. Specifically, an expected rate of patch proliferation by chance was

calculated separately for each site assuming no treatment effect and a Poisson frequency distribution of counts of patches produced by each patch initially observed until the end of the study (2014). These expected counts were then compared with observed counts. A *p*-value was obtained from 1000 pseudoreplicate expected patch counts at each site using a Microsoft Excel spreadsheet and the Macro function. Differences between the treated and the control plot were tested at each site, as were differences in the difference between treated and control plot between sites.

Responses of groundcover vegetation within patches of Japanese stiltgrass over time were analyzed by examining the responses of species richness and log-transformed densities to site, treatment, site × treatment and the product of Japanese stiltgrass density and patch age using analysis of covariance. The product of Japanese stiltgrass density and patch age (from 1 to 7 years) was an indicator of the potential competitive effect of Japanese stiltgrass on the native vegetation. Responses of the native vegetation were examined by quantifying both the change between initial and final censuses and the average of the initial and final censuses. Because the number of patches differed between sites (resulting in unequal sample sizes), we analyzed the responses using Type II sums of squares, when the site × treatment interaction was weak and not significant (*p* > 0.2), thereby eliminating the site × treatment interaction from the model and thus the bias associated with the lack of independence between the main effects of site and treatment and the site × treatment interaction. Type III (partial) sums of squares were used when the p-value associated with the site × treatment interaction was less than 0.2. All statistical analyses were done using JMP v. 5 (SAS Corporation, Cary, NC).

Results

Groundcover Vegetation Responses

The treatments were effective at increasing groundcover plant species richness and groundcover plant density. Species richness and plant density were both significantly greater in treated plots than in adjacent control plots in the fall 2013 ($F_{1,1}$ = 2416.36, *p* = 0.013 for species richness; $F_{1,6}$ = 7.07, *p* = 0.038 for log density; Figure 1). In contrast, species richness and density did not differ significantly between treated and control plots in the pre-treatment censuses (2003 for Wildflower Loop and 2007 for Sharecropper Loop; initial species richness = 33.68 vs. 22.23 per 300 m² subplot in the control and treated plots, respectively; $F_{1,1}$ = 1.49; *p* = 0.437; initial log shoot density = 3.17 vs. 2.35 per 2.25–m² sub-subplot in the control and treated plots, respectively; $F_{1,1}$ = 0.34; *p* = 0.66).

The treatments were generally effective at increasing the abundance of both open-habitat and forest species, while not increasing the abundance of ruderals (Figure 2A).
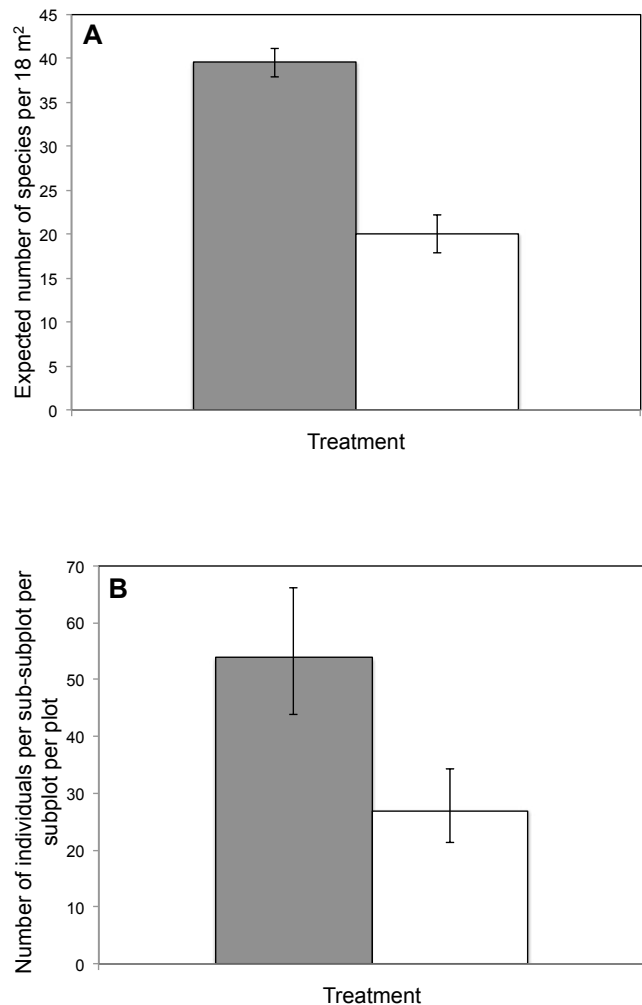

Figure 1. Effect of restoration treatments (canopy reduction combined with repeated prescribed fire) on A) groundcover plant species richness and B) density of groundcover plant stems/clumps. Values of species richness are leverage means (n = 2) estimated from species-area curves adjusted for an area of 18 m², equivalent to 8 1.5 × 1.5 m vegetation plots (the minimal number found in a plot) and ± 1 standard error. Values of density are leverage means (error df = 6) of back-transformed log densities per 1.5 × 1.5 m sub-subplot per subplot per plot and ± 1 back-transformed standard error. Filled bars correspond to treated plots, open bars to control plots. Error variance pooling for testing treatment effect on densities used a Restricted Expected Maximum Likelihood (REML) approach to avoid pseudoreplication.

In the fall 2013, weighted mean fidelity to open habitats was significantly greater in the treated plots than in the control plots ($F_{1,6}$ = 8.75, *p* = 0.025). In contrast, weighted mean fidelity to open habitats was actually lower in the treated plots than in the control plots in the pre-treatment censuses at the beginning of the study ($F_{1,1}$ = 1614.98, *p* = 0.016). Examples of open-habitat indicators that responded positively to the restoration treatments included *Helianthus* spp. (including Ozark Sunflower [*Helianthus silphioides*], a
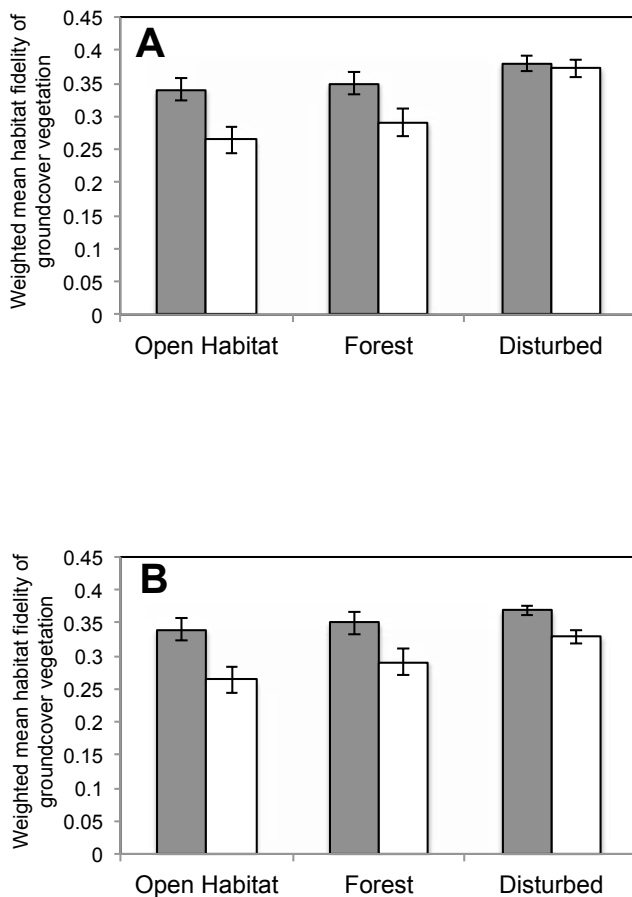
Figure 2. Groundcover vegetation composition within sub-subplots in the fall 2013 quantified using weighted mean fidelity to open habitats, forests, and disturbed habitats, A) including *Lonicera japonica* in the calculation of fidelity to disturbed habitats, and B) excluding *Lonicera japonica* from the calculation of fidelity to disturbed habitats. Filled bars correspond to treated plots, open bars to control plots. Values are sub-subplot means ± 1 standard error. Statistical analyses used a pooled error term as indicated by an REML approach. Habitat indication weights are presented in Table S2.

regional endemic), panic grasses (e.g., *Dichanthelium boscii* and *D. laxiflorum*), and numerous native legumes, including *Desmodium laevigatum*, *Lespedeza repens*, *L. virginica*, and *Strophostyles umbellata*. There was also a trend towards higher weighted mean indication of forests in treated plots than in the control plot, but the effect of treatment was not significant ($F_{1,6} = 4.62$, $p = 0.075$). Some of the species that responded positively to the treatment were indicators of both open habitats and forests, (e.g., Bosc's panicgrass [*Dichanthelium boscii*]). Weighted mean fidelity to forests appeared to be greater in control plots than in treated plots at the beginning of the study, but the power of the test was low, and the difference was not significant ($F_{1,1} = 7.10$, $p = 0.23$). Weighted mean fidelity to disturbed habitats did not differ significantly between treated and control plots in either 2013 or at the beginning of the study ($p =$
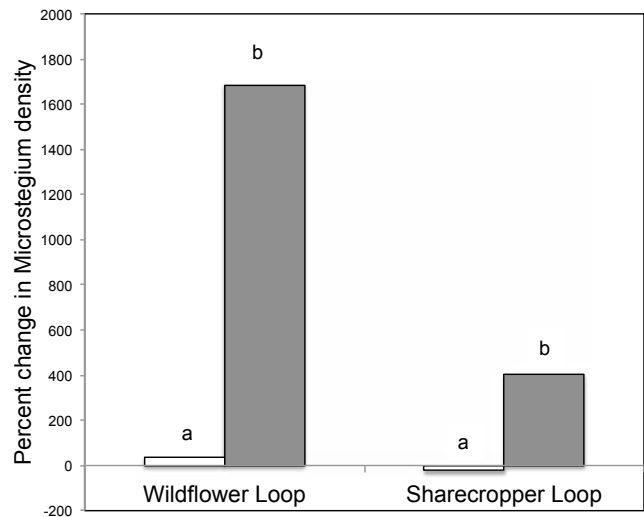

Figure 3. Percent change in density of *Microstegium vimineum* between the time of patch discovery and fall 2014 (or fall 2013 within the control plot at Wildflower Loop) within ~4 m² patches. Values are mean percent change per patch per plot. Different letters above the columns indicate statistically significant differences at the 0.05 level. Filled bars correspond to treated plots, open bars to control plots.

0.70 in both years; Figure 2A). The lack of response was largely due to the fact that Japanese honeysuckle (*Lonicera japonica*, a non-native vine somewhat indicative of forests and disturbed habitats; Supplementary Table S1), which dominated the groundcover, did not respond positively to the treatments. When this species was removed from the analysis, the treated plots had higher weighted mean fidelity to disturbed habitats than did control plots in 2013 ($F_{1,6} = 11.19$, $p = 0.016$; Figure 2B). The difference was largely due to a positive effect of the treatments on little bluestem (*Schizachyrium scoparium*) and broomsedge (*Andropogon virginicus*), both of which are moderately indicative of disturbed habitats. Habitat indication values for all groundcover plants encountered are presented in Supplementary Table S1.

Japanese Stiltgrass Abundance and Patch Establishment

The invasive grass, Japanese stiltgrass, appeared to increase in response to the treatments at both sites (Figure 3). However, the way in which the increases occurred differed between sites. At Wildflower Loop, Japanese stiltgrass increased primarily as a result of increased density within two patches (Figure 3). Three of the four patches of Japanese stiltgrass were present at the beginning of the study. A fourth was located next to the largest patch and most likely was founded by individuals from that nearby (ca. 2 m) patch. The smallest patch lost individuals and had disappeared by the 2014 measurement. The number of patches in the control plot at Wildflower Loop decreased from
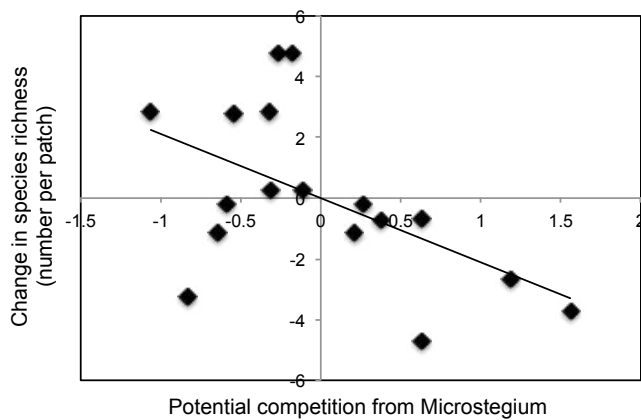
Figure 4. Responses of species richness of native groundcover species within *Microstegium* patches to potential competition from *Microstegium vimineum* (measured as the product of log *Microstegium* density and patch age in years). Y-axis values are patch mean leverage residuals of the difference between initial and final censuses and corrected for site and treatment effects. X-axis values are patch mean leverage residuals of the average densities of initial and final censuses times patch age.

4 to 2 between 2007 and 2013. The rate of loss in Japanese stiltgrass patches between the control and the treated plot was not statistically significant at Wildflower Loop ($p = 0.238$). At Sharecropper Loop, in contrast to Wildflower Loop, both the density within patches (Figure 3) and the number of patches of Japanese stiltgrass increased significantly in response to the treatments ($p = 0.003$). The number of patches in the treated plot at Sharecropper Loop increased from 2 to 9 between 2007 and 2014. In contrast, the number of patches in the control plot at Sharecropper Loop decreased from 2 to 1. Site differences in the differences in patch proliferation rates between control and treated plots were statistically significant ($p = 0.005$).

Changes in Groundcover Vegetation within Japanese Stiltgrass Patches

Native species richness decreased over time in dense patches of Japanese stiltgrass, as indicated by a significant, negative relationship between the increase in species richness and patch-age-weighted Japanese stiltgrass density ($F_{1,13} = 5.17$, $p = 0.04$; Figure 4). Although the density of native species averaged across initial and final censuses was negatively correlated with patch-age-weighted Japanese stiltgrass density ($F_{1,12} = 5.25$, $p = 0.04$), there was no evidence of a decline in density over time as a function of patch-age-weighted Japanese stiltgrass density ($F_{1,13} = 0.10$; $p = 0.75$). Neither open-habitat indicators nor ruderals responded to patch-age-weighted Japanese stiltgrass density ($p = 0.47$ and 0.30, respectively). An increase in forest indicators in response to increasing patch-age-weighted Japanese stiltgrass density approached statistical significance ($F_{1,12} = 3.76$, $p = 0.08$).
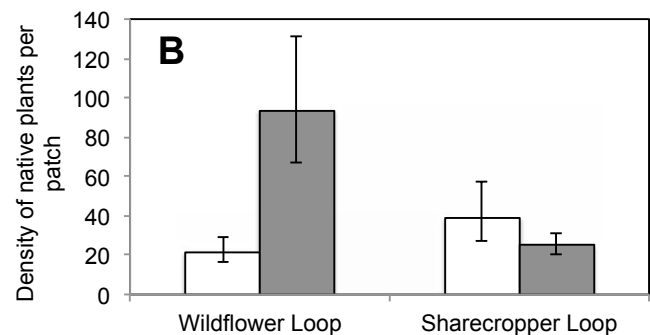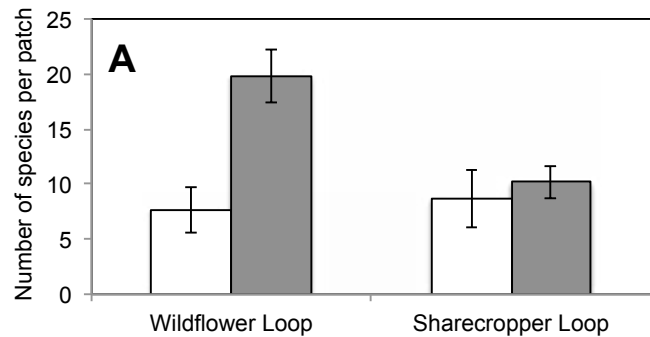

Figure 5. A) Species richness and B) density of native groundcover species within *Microstegium* patches in treated and control plots at each site. Values are patch mean leverage residuals averaged over initial and final censuses and corrected for site and treatment effects and the site x treatment interaction. Filled bars correspond to treated plots, open bars to control plots. Error bars are ± 1 standard error.

After accounting for Japanese stiltgrass density, changes in native species richness did not differ significantly between sites, nor were they significantly affected by treatment or the interaction between site and treatment ($p > 0.28$). There was a trend towards a greater reduction over time in native plant density in control plots than in the treated plots ($F_{1,13} = 3.75$; $p = 0.075$). Native species richness and density within Japanese stiltgrass patches were both greater in the treated plot than in the control plot when averaged across the initial and final censuses at Wildflower Loop but not at Sharecropper Loop ($F_{1,12 \text{ (site × treatment)}} = 4.03$ and 6.39, respectively, $p = 0.07$ and 0.02, respectively; Figure 5A, B).

Discussion

In general, the results of these groundcover vegetation surveys indicate that restoration treatments involving thinning of overstory and midstory trees combined with frequent burning increased the species richness and abundance of groundcover plant species indicative of fire-maintained open habitats. The increase resulted from the fact that

many of the desired species were already present but at low densities and suppressed by shade. Canopy reduction and fire created the environmental conditions necessary to promote the natural increase of species indicative of fire-maintained open woodlands (Clewell and Aronson 2013). This response provides support for the fire tolerance hypothesis and is consistent with a primary restoration goal in oak woodlands and forests of the eastern United States (Smith 1994, Taft 1997, Laatch and Anderson 2000, Hutchinson et al 2005, Ruffner and Groninger 2006, Kinkead et al. 2013). The restoration treatments also had what appeared to be a modest positive effect on the abundance of species indicative of forests (see also Hutchinson et al. 2005), but this trend was not statistically significant at the 0.05 level, possibly due to low statistical power. Hence, the increase in open-habitat indicators did not come at the expense of forest indicators. This observation resulted in part from the fact that some of the species that responded positively to the treatment were indicators of both open habitats and forests (e.g., *Dichanthelium boscii*). These results contradict one component of the disturbance sensitivity hypothesis, which predicts that forest species should respond negatively to fire. Matlack (2013), who criticized the use of fire in deciduous forests, argued that most deciduous forest plant species lack the adaptations to fire (e.g., smoke-cued germination, resprouting from rhizomes) necessary to respond positively to fires. It is possible that the sites studied here occurred on soils that were not as moist or fertile as those envisioned by Matlack and therefore lacked many of the forest specialists that would have responded negatively to canopy reduction and frequent fires. Groundcover vegetation in the deciduous forests studied here was tolerant of low-intensity surface fires, perhaps because many species were perennials with rhizomes, deep taproots, or belowground bud/seed banks that were protected from damage by such fires (e.g., *Helianthus*, *Desmodium*, *Lespedeza, Dichanthelium* spp.). In addition, the positive density and richness responses to canopy openings indicate that most groundcover plant species, including those indicative of forests, exhibited growth and reproduction that were strongly light limited (light-flexible species, sensu Collins et al. 1985). These results are consistent with a previous study of groundcover vegetation responses to tornado damage in oak-hickory-shortleaf pine forests in the interior coastal plain of northern Mississippi (Brewer et al. 2012). In that study, numerous forest indicators responded positively in terms of density to tornado damage, even more so than many open-habitat indicators. Furthermore, very few forest indicators (including those specifically indicative of shady mesic forests) responded negatively to tornado damage. Indeed, as a group, forest and open-habitat indicators were more likely to show positive flowering responses to canopy damage than were ruderals indicators (Brewer et al. 2012). Taken together, these results suggest that many groundcover plant species in oak-hickory-dominated forests of northern Mississippi are tolerant of canopy openings and low-intensity surface fires.

Another encouraging result of this study was the lack of a generally positive response of ruderals to the restoration treatments. Low-intensity surface fires are not severe disturbances, and thus in one sense they should not be expected to favor ruderals or other species dependent upon soil disturbances or other lethal factors (Grime 1979, Roberts 2007, Brewer and Bailey 2014). There were some native ruderals that responded positively to the treatments either initially or in years with fire (e.g., *Erechtites hieraciifolia*, *Acalypha* spp., *Phytolacca americana*). By the time of the last census of the groundcover plots (fall 2013, a year with no fire), the responses of ruderal species to the treatments was minimal. Hence, as predicted by Brewer et al. (2012), ruderal species may initially respond positively to canopy reduction and during years with fire but then diminish over time and/or during years without fire.

The lack of response of perennial ruderals to the treatments was largely due to the fact that Japanese honeysuckle, which dominated the groundcover, did not respond positively to the treatments. When this species was removed from the analysis, the positive responses of some common native perennials moderately indicative of disturbed habitats, i.e., little bluestem and broomsedge, resulted in a significant positive effect of the treatments on mean fidelity to disturbed habitats. However, little bluestem is an important fuel species for surface fires (Maynard and Brewer 2013) and provides cover for declining groundnesting bird species such as Northern bobwhite quail (Miller and Miller 2005, Brawn 2006). Hence, increases in little bluestem in response to the treatments are desirable from a management and conservation standpoint.

The positive response of the invasive non-native grass, Japanese stiltgrass, is consistent with the findings of previous studies (Glasgow and Matlack 2007, Emery et al. 2013) and is definitely cause for concern. We found that the proliferation of patches in response to the treatments was much greater at the site with a more recent history of agricultural disturbance (Sharecropper Loop). The lack of replication of sites with different land use histories, however, precludes drawing any definitive predictions regarding how the response of Japanese stiltgrass to restoration treatments will vary among sites.

Native vegetation located within patches of Japanese stiltgrass appeared to respond negatively to Japanese stiltgrass, as indicated by a reduction in native species richness in relation to the product of Japanese stiltgrass density and patch age. Hence, not only does Japanese stiltgrass have the potential to prevent succession in forests, as previously demonstrated (Flory and Clay 2010b), it can also negate positive responses of native vegetation to restoration of open tree canopies and fire. Given the beneficial effects of fire restoration on plant diversity in upland hardwood forests, the potentially negative effects of Japanese stiltgrass

on plant diversity in upland forests may be greater than previously realized (Brewer and Bailey 2014).

The observed responses of native vegetation and Japanese stiltgrass to the treatments lead us to suggest the following recommendations regarding decisions to restore fire to oak-hickory forests. Given limited resources, sites that are heavily infested with Japanese stiltgrass should be the lowest priority for restoration of fire-maintained open oak-hickory woodlands. Alternatively, for sites that have not been recently disturbed, that lack Japanese stiltgrass and that contain remnant populations of open woodland indictors, selective canopy thinning and repeated prescribed burning could be a practical and effective means of restoring plant diversity and desired species composition over the long term.

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